THE OTOLITHS OF SENESCENT KAHAWAI, *ARRIPIS TRUTTA* (ARRIPIDAE)

by

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ABSTRACT. - Two young Kahawai (*Arripis trutta,* Arripidae) were introduced into the Napier Aquarium (New Zealand) in 1975 as presumed 1-2 year old fish at about 25 cm total length. One fish died in 1987 from apparent senescence, the other died in 1989 with symptoms of senescence that included locomotory dysfunction, exophthalmia and fusion of the spinal vertebrae into a rigid mass. Both fish were aged by scale annual marks: the first was aged at 14 years, the second at 16 years; both being the expected age. The patterns of spacing of scale age marks (annual checks) in the first fish corresponded to the known temperature fluctuations in the aquarium. The otolith contained 20 checks in the sulcul part of the otolith of the type that have been regarded as annual in this and other species. The otolith of the second fish also contained 19 to 20 annual type check rings in the sulcul part of the otolith. Fifty, or more, checks that correspond to those specifically described by other workers as annual in the Kahawai otolith were observed in the ventral anti-sulcul growth axis of the otolith. A map of the calcium density of a cross section of the first fish otolith by proton microprobe showed fourteen peaks whose widths corresponded to those of the annual checks of the scale.

RÉSUMÉ. - Deux jeunes Kahawai (*Arripis trutta,* Arripidae) ont été introduits dans l'Aquarium de Napier (Nouvelle-Zélande) en 1975 à l'âge de 1 ou 2 ans et à une longueur totale de 25 cm. L'un d'eux est mort apparemment de vieillesse en 1987 et l'autre en 1989 présentant aussi des symptômes de vieillesse: locomotion difficile, exophthalmie et fusion des vertèbres en une masse rigide. L'âge de ces deux individus a été estimé par scalimétrie. Le premier avait 14 ans, le second 16, ces deux valeurs étant les âges attendus. L'espacement des marques annuelles sur les écailles du premier individu correspond aux fluctuations connues de la température dans l'aquarium. Le sulcus de l'otolithe présente 20 marques du type considéré comme étant annuel chez *Arripis trutta* et d'autres espèces. Le sulcus de l'otolithe du second poisson contenait aussi 19 à 20 marques de ce type. Cinquante marques ou plus, correspondant à celles qui ont été décrites par d'autres auteurs comme annuelles dans l'otolithe du Kahawai, ont été observées dans l'axe ventral de l'anti-sulcus. La densité de calcium, mesurée à l'aide d'une microsonde ionique dans une section transversale de l'otolithe du premier poisson, montre 14 pics dont l'épaisseur correspond à celle des marques annuelles relevées dans les écailles.

Key-words. - Arripidae, *Arripis trutta,* Aquarium, Otoliths, Checks, Microincrements, Senescence.

Fishes probably rank second only to humans in the amount of material published on their age. For example, Beamish and McFarlane (1983) reviewed over 500 papers on estimating age in fishes. Although not in such numbers, there have been many papers published on the physiology of the ageing and senescence process in fish (Craig, 1985; Finch, 1990). Organ-specific senescence has been described in many species, but little or no information is available about otoliths from senescent fish. Consequently, we have little information about the effects of senescence on otoliths of large, commercially

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desirable marine species. Included in those unknowns are the effects of senescence on the ultrastructure of the otolith. In this paper we describe otolith ultrastructure and calcium chemistry from two large specimens of the kahawai, *Arripis trutta* that died of senility in aquarium conditions.

Teleost otoliths were shown by Carlstrom (1963) to be composed of calcium carbonate, usually in the form of the mineral aragonite, crystalized on an organic matrix composed of a protein, otolin, that is rich in aspartate and glutamate residues (Degens *et al.*, 1969). In some fish otoliths a seasonal variation in the mineral to protein ratio occurs resulting in a series of opaque zones with more protein, alternating with hyaline (translucent) zones with less protein (about 0.25% compared with about 0.17% (Mugiya, 1965)). As a result of this seasonality, series of opaque and hyaline zones in the otoliths have been used to estimate the age of some fish species (Bagenal, 1974).

The kahawai, *Arripis trutta*, occurs in both New Zealand and Australian waters. There is a considerable discrepancy between scale and otolith-based ages assigned to this species; maximum otolith age being 22+ (Eggleston, 1975), and maximum scale ages ranging from 10+ (Eggleston, 1975) to 9+ (Nicholls, 1973). Two small kahawai (25 cm total length) were placed in the Napier (New Zealand) Aquarium in 1975. In 1987 one fish died of old age. The second died of similar symptoms in 1989. This offers a rare opportunity to examine the otoliths and scales of individual fish which were known to be at maximum physiological age, and to compare the observations with both the specific expectations of kahawai ageing, and the more general expectation of the ultrastructure of "old" teleost otoliths.

MATERIALS AND METHODS

Kahawai otoliths were cut in half in the vertical plane (i.e. medio-lateral plane *in situ*) and sections mounted with epoxy resin on stainless steel pin mounts. One-half was then lightly etched in ethylene diaminotetracetic acid (EDTA) 0.1M pH 2.0 for 60 seconds and the etched surface photographed with a Philips 505 Scanning Electron Microscope (SEM), after sputter coating with gold. The other half of this otolith was mounted on a glass slide and ground down to provide a thin (50 µm) optical section using 4000 grit wet and dry paper on a Struers pedemax petrographic grinder. The thin otolith section was photographed with crossed polarizing filters to enhance crystal resolution. A whole otolith from the second fish was mounted sulcus-upward and photographed by a Philips 505 SEM after sputter-coating with gold. After photography, the glass slide was cut to fit an aluminum sample holder and the specimen was scanned 400 times with a proton microprobe following the methods of Coote *et al.* (1982). The proton microprobe technique energizes atoms with impact from high speed proton beams resulting in emission spectra characteristic of each element. The spatial variation in elemental composition, i.e. density of the element, is therefore measured as changes in the count-rate of emissions at specific frequencies. The calcium count density was converted into a three dimensional map using a LOESS smoothing technique (Cleveland, 1979; Cleveland and Devlin, 1988; Cleveland *et al.*, 1988). The LOESS technique is designed to remove short period noise to show the underlying functional relationship without the need to fit the data to an *a priori* parametric function. Scales were used to estimate age following the methods described in Gauldie *et al.* (1990) and their nomenclature is used in this paper.

Temperature and salinity records from December 1978 to November 1987 were obtained from the daily records maintained by the Napier Aquarium (pers. comm. W. Watkins and R. Yarrell, curators, Napier Aquarium).

Ageing conventions

Ageing conventions based on otolith ultrastructure have usually evolved by consensus as to how to interpret the patterns of ultrastructural marks in any particular otolith by reference to what is believed to be an annual pattern observed in otoliths from marked or known age fish (Keir, 1960). Annual otolith ageing conventions do not depend on distinguishing an "annual" from a "non-annual" mark by some chemical or other innate quality, but by a certain pattern of the marks (Gauldie, 1988). Consequently the language used to describe annual marks carries a significant meaning only within the ageing convention that describes the pattern of such marks. In this study we refer to optical aretched marks in the otolith as checks if they have spacings > 5 µm, or as microincrements for spacings < 5 µm. This nomenclature is neutral, but arbitrary and is intended to be read only in the context of this study.

A change in interpretation of what was an opaque zone occurred sometime between Dannevig's (1956) description of the effects of burning on the wide opaque zones of cod otoliths, and the assumption that narrow opaque check rings in the burned otolith of the sole and other fishes were equivalent marks to the cod opaque zones (Christensen, 1964). In subsequent papers, check rings, as opposed to opaque zones, were assumed to be annual and described as occurring in both the medio-lateral and the sulcul aspect of the otolith (Wiedemann-Smith, 1968). This change in interpretation proved to be very significant because, in some cases, the use of check rings (particularly those in the sulcul part of vertical sections of the otolith) as opposed to opaque and hyaline zones conventionally read in horizontal sections of the otolith, lead to the conclusion that species such as the New Zealand snapper *Chrysophrys auratus*, and the Pacific Ocean perch *Sebastes alutus*, were very much longer lived than previously thought (Paul, 1976; Beamish, 1979). The differences between estimates of age based on opaque zones and upon sulcul check rings have been explained by postulating that at a certain age the otolith stops growing in the medio-lateral plane but continues to grow in its sulcul part (Beamish, 1979).

Some species of fish have check rings in the sulcul side of the otolith that have been shown to be not annual. These include the blue fin tuna (Lee *et al.*, 1982), the percoid *Lateolabrax japonicus* (Irie, 1957) and the chinook salmon (Gauldie, 1991). Opaque zones observed in whole otoliths have proved not be annual in some species, e.g. the alfonsino *Beryx splendens* (Ikenouye, 1969) and the orange roughy *Hoplostethus atlanticus* (Gauldie, 1987; 1988). However, opaque zones in the oyster toadfish otolith have been shown to be annual (Radtke *et al.*, 1985) and, furthermore, the opacity of the zone has been shown to be caused by changes in the relative amount of organic material modulated by variation in the width of daily growth increments.

RESULTS

Senility

Prior to being found dead in the aquarium, the kahawai in the Napier Aquarium progressively developed signs of locomotory dysfunction (i.e., excessive rolling in the water and swimming head downwards or with a pitching motion), as well as whitening of the body colour and both exophthalmia and mild cataract in the eyes. These are all indications of senility in fish (Liu and Walford, 1969). On 14 November 1987 the first fish was found dead in the bottom of the main tank. The fish was measured at 65.3 cm fork length. Autopsy showed that it was a male in good condition but with atrophied gonads and with no obvious signs of internal disease, parasites or internal lesions. However, the spinal vertebrae were fused together into a rigid mass. We conclude that the fish had died of old age. The second fish was found dead on the 6th March 1989. The fish was measured at 66.5 cm fork length. Autopsy showed it to be a female in good condition but with reduced gonads (3.2% of total body weight) and with no obvious signs of internal disease parasites or internal lesions. As with the first fish, the spinal vertebrae were fused into a solid mass. We conclude that this fish also died of old age. Ossification of vertebral column indicated a change in calcium metabolism associated with senility. Both fish were large for New Zealand kahawai, but following the key of Whitley (1951), it was confirmed that the fish were from the New Zealand species *Arripis trutta* and not the larger Australian sub-species *Arripis trutta esper*.

Age comparison

Scales

A sample of 25 scales was taken from each fish posterior to the pectoral fin in the area of the lateral line canal, about half-way between head and tail. Scales from this region have been shown to have the least errors associated with scale reading (Dannevig and Host, 1931). In the first fish, three scales showed clear checks of the kind conventionally used in fish ageing (Kelley, 1988), including the kind figured by both Eggleston (1975) and Gauldie *et al.* (1990) for kahawai scales. The remaining twenty-two scales showed no checks and appear to correspond to the type of scale described as "erosion" or "replacement" scales, but were not in significantly greater proportions than those found in old fish of other species (Paget, 1920) as well as kahawai (Gauldie *et al.*, 1990).

The year in which the first fish was spawned, as projected by scale ageing, was 1973. Both otolith and scale ages predict that a 25 cm fish would be between 1 and 2 years old (Eggleston, 1975). As the fish was caught in 1975, the scale-based date agrees well with the 1973 projected date of spawning. Five scales from the sample of 25 scales taken from the second fish showed clear checks. Four scales were counted as having sixteen checks, and the fifth as fifteen checks.

The width of the spacing between scale checks for the first fish and mean daily water temperature from the Napier Aquarium records are plotted against year in figure 1a.

Otolith check rings

The otolith of the kahawai was longer (anterior-posterior) than wide (dorsal-ventral). The anterior dorsal half of the otolith had a prismatic structure. Dorso-ventral sections of the otolith were made through the center of the longest dorsal prism, along the dorso-ventral axis through the nucleus of the otolith.

The SEM pictures of etched sections of the otolith from the first fish had a complex internal structure (Fig. 2a). The ventral (*in situ*) edge of the otolith section was flattened compared to the dorsal edge, reflecting growth restriction at the point where the ventral edge of the otolith lies on the skull bones that form the floor of the otic capsule.

Detail of the ventral part of the otolith section showed that it was divided by a crystalline anomaly into a sulcul and anti-sulcul component (Fig. 2b) resulting in the familiar pattern of four growth quadrants or axes in the dorso-ventral section of the otolith. Twenty checks could be counted in the sulcul ventral growth axis, and at least 50 check rings could be counted in the anti-sulcul ventral growth axis (Fig. 2b).

Detail of the dorsal side of the otolith showed that it was also divided into a sulcul and anti-sulcul half by a crystalline anomaly (Fig. 2c). Twenty check rings could be counted (with difficulties) in the sulcul dorsal growth axis but up to 50 checks could be readily counted in the anti-sulcul dorsal growth axis

The width between the checks in the sulcul ventral growth axis of the otolith section progressively decreases from the nucleus to the sulcul edge of the otolith (Fig. 2b). A plot of the cumulative width between these checks is shown in figure 1b. Cumulative width against check number has the form of an asymptotic curve which approaches a limiting value for maximum cumulative width.

The method of Eggleston (1975) involved grinding the ventral edge of the otolith in the plane of anti-sulcul ventral growth axis to reveal annual checks. Although the method was not described in detail, nor the criteria for what was an annual check given, it is clear from figure 2b that the number of check rings observed by the method of Eggleston (1975) would have depended on the extent of grinding and the degree of

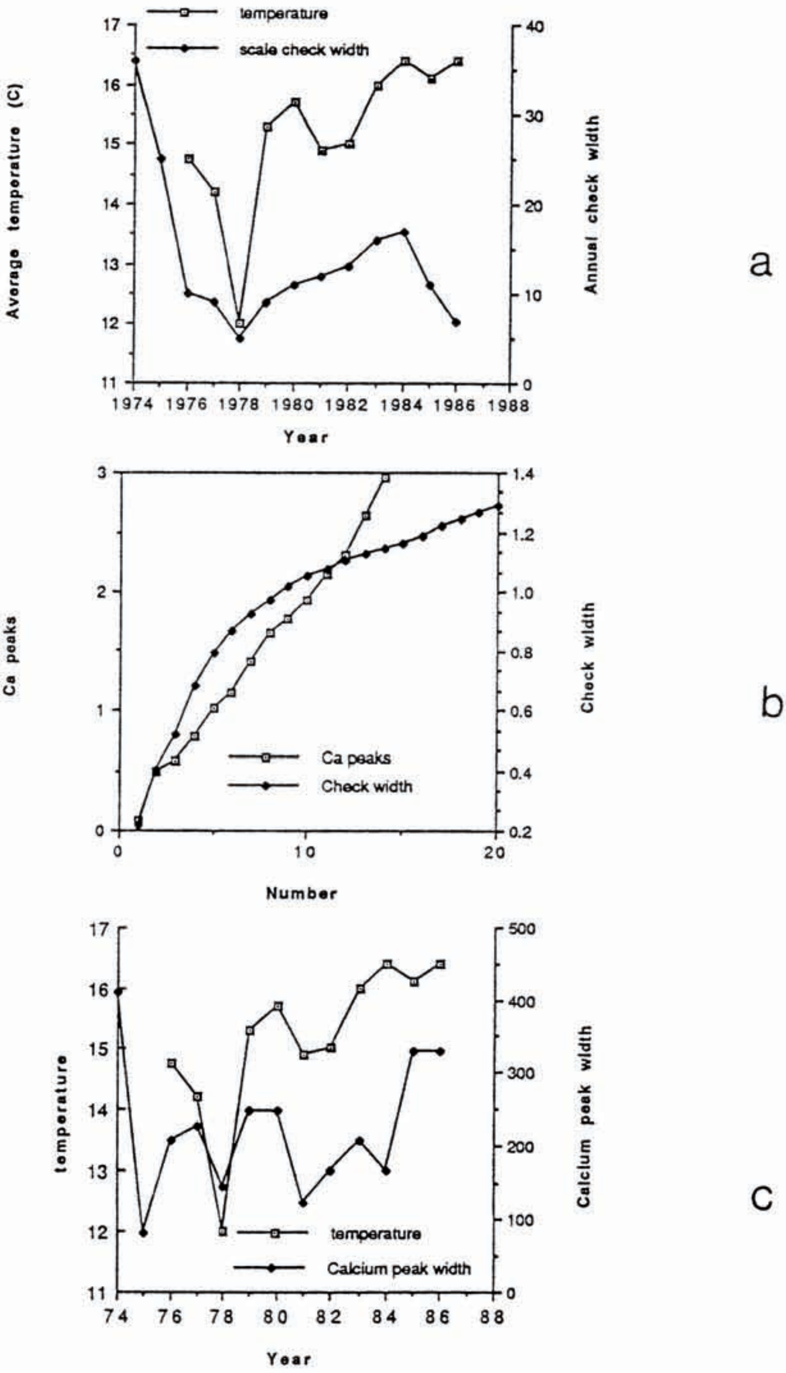

Fig. 1. - a. - Widths between scale checks (annual check width) and mean daily water temperature (average temperature) are plotted against year. b. - Cumulative widths are shown for scale checks (check width) and otolith calcium peaks (Ca peaks) plotted against the sequential number of the check or the peak. c. - Widths between otolith calcium peaks (calcium peak width) and daily water temperature (temperature) are plotted against putative year of otolith deposition.

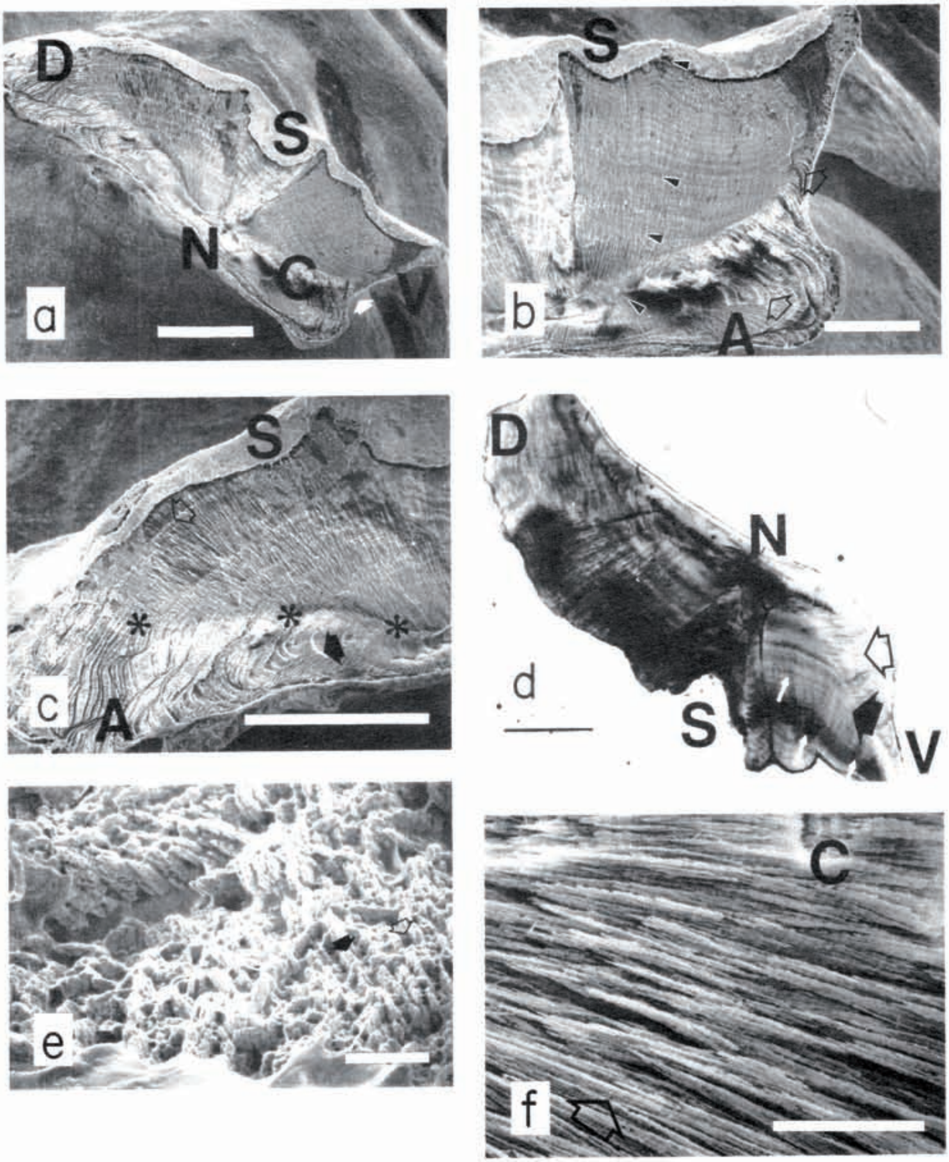

Fig. 2a.- An SEM of the etched section of the first kahawai otolith shows a well developed sulcus (S) that divides the otolith into a dorsal (D) and ventral (V) section. The sulcus begins near the nucleus (N) but has been filled-in with layers of crystalline material. Both the dorsal and ventral parts of the otolith are further divided into sulcul and anti-sulcul sections by a line of crystalline anomaly (C). The section shows growth restriction at the ventral edge with narrowing and turning (arrow) of the ventral anti-sulcul growth axis. Bar = 1 mm. b.- Detail of the ventral part of the otolith section showing a crystalline anomaly marking the division of the otolith into sulcul (S) and anti-sulcul (A) sections. Twenty checks (outlined arrows) could be counted in the sulcul ventral growth axis of the otolith. There were more than fifty check rings in the anti-sulcul ventral growth axis (arrows). Bar = 1 mm. c.- Detail of the dorsal part of the otolith section showing the division into sulcul (S) and anti-sulcul (A) sections by a crystalline anomaly (asterisks). Twenty checks could be counted in the sulcul dorsal growth axis of the otolith (open arrow), but up to fifty in the anti-sulcul dorsal growth axis (arrow) of the otolith. Bar 1 mm. d.- An optical section along the dorso-

magnification. However, under the best interpretation, Eggleston's method would have ground deeply enough to reveal only the check rings in the anti-sulcul ventral growth axis of the otolith that contains a large number of check rings (50 in Fig. 2b). These are not analogous to the annual checks described in the sulcul ventral growth axes of the otoliths by Paul (1976) and Beamish (1979). Only twenty of the "annual" checks of the type described by Paul (1976) and Beamish (1979) occurred in the sulcul ventral growth axis of the kahawai otolith (Fig. 2b).

The division of the otolith into a sulcul and anti-sulcul half by a crystalline anomaly raises the question of whether or not these two halves of the otolith are physiologically separate. Detail of the boundary between the anti-sulcul dorsal growth axis and the sulcul dorsal growth axis shows that some check rings are homologous and continue through the crystalline anomaly from sulcul to anti-sulcul side (Fig. 2c).

An optical section of an otolith from the second kahawai showed that nineteen or twenty checks could also be counted in the sulcul ventral growth axis of the otolith in optical sections (Fig. 2d). Although less clear than in SEM sections, up to 50 checks could be counted in the anti-sulcul ventral growth axis of the otolith (Fig. 2d). In addition, cross polarization reveals the structure of the crystals that make up the otolith. Regular crystal growth occurs from the nucleus along the dorsal anti-sulcul axis, but crystal growth from the nucleus to sulcul (i.e. inward facing) surface was irregular with a jointed crystalline habit (Fig. 2d).

The surface of the otolith was also examined for any signs of perturbation of calcium deposition at the point of death. The sulcul surface of the otolith showed rounded crystals arranged in the form of stacked lamellae (Fig. 1c). Measurements of the widths of lamellae showed that the protruding lamellae were the narrower lamellae (about 0.9 µm average width range 0.45-1.9 µm) rather than the recessed wider lamellae (about 1.65 µm average width range 0.9-2.75 µm).

Otolith microincrements

Microincrements of the same size and appearance as the daily microincrements described for the otoliths of other species (Campana and Neilson, 1985) occurred in the growth axis in the anti-sulcul part of the dorsal side of the otolith. The average width of microincrement was about 2.0 µm in the growth axis in the anti-sulcul part of the otolith (Fig. 2f). However, the growth axis in the anti-sulcul part of the otolith is characterized by a large number of checks amongst which it is difficult to discern microincrements because of the strong etching effect associated with checks.

Calcium density

Calcium density in both the anti-sulcul and sulcul quadrants was measured by proton microprobe analysis as calcium counts per unit area. Calcium density data was smoothed using the LOESS technique.

The smoothed three-dimensional map of calcium count density was further enhanced by raising the calcium floor (Fig. 3). The calcium map is viewed with the sulcus side to the front right and the anti-sulcus side to the rear left. The map shows a series of ridges of calcium counts running from anti-sulcul to sulcul side. The nucleus is

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ventral axis (D,V) through the nucleus (N) of the second kahawai otolith showing checks in the sulcul ventral growth axis of the otolith (arrow) as well as in the anti-sulcul ventral growth axis (open arrow). The cross polarization shows regular growth in the sulcul (S) side of the dorsal section, and jointing (small arrows) in the ventral section of the otolith. Bar = 1 mm. e.- An SEM of the sulcul surface of the kahawai otolith showing rounded crystals formed into protruding (arrow) and recessed (open arrow) lamellae. Bar = 20 µm. f.- Microincrements occur in the anti-sulcul dorsal growth axis of the otolith (arrow). Check rings appear as more deeply etched structures (C) that sometimes fail to interrupt the progressive growth of microincrement layers. Bar = 100 µm.

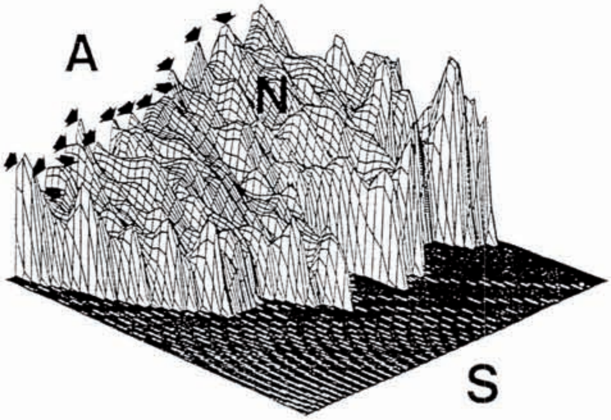

Fig. 3. - The calcium surface of the section of kahawai otolith is oriented with anti-sulcul edge (A) to the left rear and sulcul edge (S) to the right front. The nucleus (N) is located in a hollow in the center of the section. Calcium peaks along the anti-sulcul dorsal growth axis are marked with arrows. The maximum calcium count is 583 with the floor set at 450.

in a pit in the central part of the calcium density map and there are fourteen peaks in calcium along the anti-sulcul edge towards the nucleus. The calcium counts along the ventral edge are organized into relatively few peaks (Fig. 3). Measurements of the widths between calcium peaks are plotted against putative years of deposition in figure 1c to facilitate comparison with both water temperature records, and the widths between putative annual checks in scales (plotted in Fig. 1a). The cumulative change in widths between calcium peaks is shown in figure 1b for comparison with the cumulative widths between scale check rings also plotted in figure 1b. The difference in numbers of points reflects the higher numbers of scale check rings than otolith calcium peaks.

DISCUSSION

Aquarium reared fish provide the only realistic means of studying senility in fish. Aquarium reared fish have been used as models for the basic biology of vertebrate senility (Gerking, 1959; Comfort, 1961), although the study of senility in aquarium reared fish may depend on the amenability of the fish to aquarium conditions. A summary of maximum ages attained by aquarium fish (Hinton, 1962) showed that cartilaginous fishes were generally longer-lived than teleosts, although some teleost species survived for 20+ years. Although senescence in fish can be identified (Liu and Walford, 1969) and is obviously an important issue in fish age theory (Comfort, 1961), none of the 500 plus papers quoted in a review of fish ageing by Beamish and McFarlane (1983) deal with senescence. Both of the kahawai used in this study were very large, much larger than the maximum size recorded for this species by either Eggleston (1975) or Nicholls (1973). Apart from the physiological dysfunction due to apparent old age, both fish were in good condition. Their putative ages, 15 and 16 years, would make them long-lived by the standards of aquarium reared teleosts (Hinton, 1962). The symptoms of the kahawai prior to death in 1987 and 1989 were consistent with death being due to old age.

However, signs of extreme senescence (lordosis, kyphosis and emaciation) which have been observed in other fishes (Liu and Walford, 1969) were not present, so that although senile, these fish may not have been at the extreme of old age for the species. However, it is rare to find such large fish that have reached senility, even in aquaria. In the wild it is even more rare to find fish whose ages are much greater than normal upper age limits usually assigned to the species (Galligan, 1959). The recovery of fish that had died of senility in the wild is most improbable. Apart from the low probability that any fish might survive to its maximum physiological age, there is also the efficiency with which scavengers remove dead fish (Smith, 1986). In the case of the kahawai we have a rare opportunity to examine the scales and otoliths of fishes whose age and temperature life histories are known and which also show all the signs of having reached maximum physiological age.

The age assigned to the fish from scale annual checks was consistent with the fish being 1-2 years old at capture; which is an appropriate age from both scale and otolith methods (Eggleston, 1975) for their size at capture. The spacing between annual checks from the scales of the first fish had a similar pattern to that of the change in ambient annual temperatures based on the ages assigned to the annual checks. The spacings between annual checks are known to grow more or less wide according to temperature in other species (Kelley, 1988). Kahawai scales also show cycles in fluorine and calcium and the patterns of checks can be related to temperature (Gauldie *et al.*, 1990). There is a good match between the spacing of annual checks in the scale and ambient temperature that supports the interpretation that scale checks delineate annual events.

The assignment of peaks and troughs of periodic structures used for aging techniques depends on pattern recognition which is always, in varying degrees, subjective (Chang, 1982; Beamish and Fournier, 1981; Keir, 1960). In the construction and examination of otolith maps of chemical density our identification of meaningful peaks and troughs has a subjective component. No non-subjective recognition of peaks and troughs exists, because, even if one accepts every turning point in the fitted surface as a meaningful peak or trough their very existence depends on the prior decision as to how the surface was to be fitted.

We favour the LOESS technique for surface construction because the fitted value at any point is dependent on nearest neighbour data points (in our case the 50 nearest neighbours, all of which are independent proton microprobe readings). Thus a feature such as a turning point only appears if it reflects trends expressed in the neighbouring data observations. However, the assessment whether the turning point has meaning still has to be made by human evaluation.

The variation in calcium density along the anti-sulcul growth axis of the otolith showed the same number of peaks as the anticipated number of years. Seasonal variation in protein content in the otolith would result in changes in calcium density on an annual basis. Staining techniques and proton microprobe analysis of the organic content of the otoliths of other species has shown apparent annual cycles in calcium (or mineral) to protein ratios (Irie, 1957; Mugiya, 1965; Gauldie, 1991). The width between peaks in calcium showed a similar pattern to the pattern of variation in mean daily water temperatures for each year. These similarities strongly support the use of both scale checks, and changes in otolith calcium levels as age estimation techniques in the kahawai.

The checks observed in both the sulcul part of the otolith and in the anti-sulcul growth axes of the otolith could be clearly counted in both optical and SEM sections. There are evidently too many checks for them to be ascribed to annual events.

The kahawai otolith showed an increase in check ring frequency towards the edge of the otolith. This is a common feature of otoliths, and check ring frequencies rise sharply at the edge of otoliths from the largest individuals of fishes from a number of different species (Gauldie, 1988; Paul, 1976; Eggleston, 1975). The common convention of growth in fishes, the von Bertalanffy curve, anticipates growth increments converging to an asymptote. Cumulative widths between check rings in the kahawai otolith has an asymptotic form similar to that of the von Bertalanffy curve. However, in the kahawai such check rings are not related directly to age, and both check rings and the von Bertalanffy-type curve may reflect a dependence on metabolic changes as has been suggested for other species (Gauldie, 1990a). The frequency of checks in all parts of the kahawai otolith does increase with age, as convention expects, but it is an increase in the frequency of checks per year, not an increase matching in the number of years. A similar situation occurs in the otolith of the blue fin tuna for which it has been shown that the increase in check ring frequency towards the edge of the sulcus part of the otolith is not linearly related to age (Lee *et al.*, 1982).

The sulcul side of the ventral part of the second otolith showed jointing which indicates recrystalization from re-nucleation sites. Jointing therefore indicates discontinuous growth, because re- nucleation requires crystal growth to have stopped and started again. Jointing suggests that the potential for local variation in crystal growth in the otolith is high. One way to test for local variation in crystal growth is to measure the width of the lamellae that form the basic growth units of crystals (Nielsen and Christoffersen, 1982). Direct measurements of growth differences between protruding and recessed lamellae showed differences in width of 0.9 µm and 1.65 µm respectively. If we assume that the basic crystal growth units differ in proportion to lamellae widths, then the volumes of growth cubes (0.9^3 µm^3 and 1.653 µm^3) differ by a factor of 6.2. The protrusion of the thinner lamellae is thereby explained by differences in crystal growth, not erosion. If erosion had occurred, the thinner lamellae would have dissolved faster, having a higher surface area to volume ratio. This is a somewhat surprising conclusion. Otolith mineral has been shown to be absorbed by fishes in extreme stress (Mugiya and Uchimura, 1989). Checks in some species may arise from metabolic stress related to calcium deposition (Campana, 1983) that is sometimes related to the rate of change of ambient temperature (Gauldie and Radtke, 1990). Although the kahawai may have had some perturbation in their calcium metabolism indicated by their fused vertebrae, the growth of the otolith does not appear to have been affected. This is an important observation because it is often assumed that growth at the edge of the otolith ceases in old fish but continues on the sulcul face. This assumption does not appear to hold true in kahawai otoliths, even in the metabolic extremes of senescence.

In common with some other species (Gauldie, 1990b; 1991) the otolith of the kahawai had a different pattern of checks in the anti-sulcul side than in the sulcul side, even though some of the checks run through the crystalline anomaly that separates both halves of the otolith. These differences in pattern indicate that growth in one part of the otolith is out of phase with the other. Phase differences are likely to indicate differences in underlying growth processes, and therefore differences in the kinds of information stored in different parts of the otolith. We should be careful not to see check rings simply in terms of either otolith or scale ages, because the pattern of check rings may contain valuable supplementary information on the pattern of metabolic events in the life of the fish (Gauldie and Nelson, 1990a).

The use of otoliths in kahawai ageing is confused even more by the microincrement patterns observed in the otolith. The microincrements observed in the kahawai otolith are similar in appearance and size to the daily microincrements observed in otoliths of other species. Their average width (2 µm) would require a growth axis 10 mm long for a fourteen-year-old fish. The growth axis of the anti-sulcul side of the most dorsal prism in which usable daily microincrements are usually deposited (Radtke, 1987; Gauldie and Nelson, 1990a) is short in the kahawai otolith, and when etched shows a complicated layered structure that may obscure very small microincrements. With further exploration of the otolith the kahawai may join the oreosomatids (Davies *et al.*, 1988) in being unsuitable for microincrement ageing because of a combination of crystalline complexity and small microincrement width.

A large part of the theory of ageing fish involves extrapolation of information collected from a small part of the otolith or scale, and thus a short time frame, to larger parts of otoliths and scales which are thought to have grown over a larger time frame. These extrapolations often leave us in the position of not being able to distinguish large fish from old fish, unless we make assumptions about the physiology of fish in which we equate size with age. Under such circumstances fish known to be physiologically old (such as the kahawai used here) whose age and life histories are well known, assume a particular importance because they allow direct tests of our assumptions. In these two specimens, at least, otoliths are indicated as retaining physiologically competent calcium metabolism, even when there were clear signs of dysfunction in calcium metabolism in the bony vertebrae; the multiplicity of check rings observed in the sulcul part of otoliths may not always be related to age.

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